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The production of arthropods on dead wood of spruce and beech in typical central European forests during the first five years after the breakdown of the trunks

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During a five year field study quantitative data were obtained on the fauna of freshly fallen trunks of spruce and of beech trees in typical stands of central Europe. On spruce the dominant fauna contained of Scolytidae, Acari, Collembola, and Sciaridae. On beech the dominant fauna contained of Scolytidae, Acari, Collembola, Sciaridae, and additionally of Formicidae, *Pityophagus ferrugineus* (Col., Nitidulidae), and of *Lymexylon navale* (Col., Lymexylonidae).

In total spruce trunks were settled in higher densities then beech trunks. In contrast to this a more diverse fauna was found on beech trunks then on spruce trunks which is shown for Diptera as an example. During the first years of degradation *Ips typographus* and *Pityogenes chalcographus* were the pioneer bark beetles which infested spruce trunks. Other bark beetle species as *Crypturgus hispidulus* follow them after a few years.

Two years after the beech trunks were fallen the highest densities of *Taphrorychus bicolor* (Col., Scolytidae) were found and several predaceous species follow. After 3-4 years of degradation the faunal composition changes deeply and e.g. on beech trunks Isopoda become more important.

The ecological roles of Scolytidae and their natural enemies are pointed out.

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Introduction

In central European forest ecosystems dead wood is one of the characteristic components. It is produced by varies sources e.g. like wind unpredictably in space and time (Nicolai 1994). During the regeneration cycle of central European forest ecosystems different amounts of dead wood were measured per area ranging from 5 % of the total biomas per area during the rejuvination time up to 70 % of the total biomas per area during the breakdown phase (Möller 1993). The present practise of management in German forests reduces this amount of dead wood per area to a minimum. However dead wood is settled by a high number of different and highly specialized organisms, and in Germany about 1500 species of funghi and about 1350 species of beetles are known to live exclusively on dead wood of different quantity and quality (Möller 1993). The present managing practise in German forests may be seen as the reason that about 60 % of these species are endangered (Andersson & Hytteborn 1991; Geiser 1986).

In this century in central Europe several times spruce plantations were blown down through storms e.g. in the 1940 ties (Bombosch 1954). These events resulted in outbreaks of bark beetles living on spruce (Wellenstein 1954) and the last gradation was registered after the storms in the winter of 1990 (Sperber 1990). At that time about 60 million m^3 of wood were blown down in Germany during a few nights. Since that time the fauna of dead wood of spruce and of beech was monitored quantitatively. The aims of this study were: to compare the different arthropod fauna on spruce and beech on areas which are representative for the present situation in German forests; to show the change of the arthropod fauna during the degradation of dead wood in time; to show possible interactions of the arthropod fauna.

Materials and methods

The investigations were carried out in forests near Marburg, Germany (50°48'N, 8°48'E). The first stand was a planted pure spruce stand (*Picea abies*) of about 88 years in 1990 at 320m a.s.l. During heavy storms in the winter of 1990 this stand was blown down nearly complete as many other pure spruce stands in Germany (Sperber 1990).

The second stand was a mixed beech-oak stand (*Fagus sylvatica, Quercus robur*) within about 15 km distance. This stand was 145 years of age in 1990, at 350 m a.s.l., and is part of a nature reserve without further management. During the heavy storms of 1990 single beeches and groups up to ten trunks were fallen creating single treefall gaps up to small openings in the closed canopy. The study sides were already described in more detail (Nicolai 1995a). In both stands further trunks were blown down during the winters at 1991/92 and 1992/93. In the years 1991-1995 bark eclectors were placed on 19 different fallen spruce trunks and on 21 different beech trunks in the study areas described. In total 30 bark eclectors were used to collect the emerging Scolytidae and other arthropod species out of the trunks. The bark eclectors contain of dark cages made out of dark plastic material with an area of 800 or 1000 cm^2. They are fixed on the bark surface of the trunks and chinks were carefully filled using black silikon. Arthropods emerging out of this darkened surface of the trunks were collected in white plastic boxes which are the only source of light into the dark cages. This gives quantitative data on the emerging arthropods per area of a fallen trunk. All bark eclectors were controlled once per week during the summers of 1991-1995 and monthly during the winters. All emerged arthropods were collected, counted, and identified in the laboratory. The method was described in more detail by Nicolai (1995b). Statistics follow Mühlenberg (1993).

Results

Tab. 1 presents the dominant fauna which emerged out of the spruce trunks during 1991-1995 (>5 % of all collected arthropods during one year at least) (n=30707). The bark beetles *Ips typographus, Pityogenes chalcographus, Xyloterus lineatus* and *Crypturgus hispidulus* and additionally mites, springtails,

Tab. 1. The dominant fauna (%, >5 % of all collected) emerged out of dead spruce trunks 1991-1995 (n = 30.707).

	1991	1992	1993	1994	1995
Acari (excl. Oribatei)	7.4	4.2	1.3	10.4	2.5
Oribatei	5.8	5.6	7.8	1.8	10.3
Collembola	12.9	44.5	38.9	21.2	67.8
Ips typographus	3.1	1.4	1.2	24.7	0.9
Pityogenes chalcographus	36.3	6.8	7.0	4.2	0
Xyloterus lineatus	7.5	0	0.04	0	0
Crypturgus hispidulus	0.9	21.2	29.0	34.0	13.8
Sciaridae	12.8	9.1	4.0	0.2	0
Sum (%)	86.7	92.8	89.24	96.5	95.3
area (m^2)	9000	12600	12600	11800	8200
n (of all)	5984	12443	2400	7126	2754
n/m^2	6648.8	9875.4	1904.7	6038.9	3358.5

and sciarid flies made the dominant fauna which emerged out of the spruce trunks with high percentage values. In total these groups made more than 86 % of the total collected fauna in each year. During the years the percentage values of *P. chalcographus*, *X. lineatus* and *I. typographus* decreased, and the values of *C. hispidulus* increased up to 1994 and decreased again 1995. The calculated emerge rate per m^2 of spruce trunks were 1904.7 up to 9875.4 animals per m^2 and per year (Tab. 1). Tab. 2 presents the dominant fauna which emerged out of the beech trunks during 1991-1995 (>5 % of all collected arthtropods during one year at least) (n=11784). The bark beetles *Taphrorychus bicolor* and *Xyloterus domesticus* and additionally mites, springtailes, *Pityophagus ferrugineus* (Col, Nitidulidae), *Lymexylon navale* (Col., Lymexylonidae), sciarid flies and ants made the dominant fauna which emerged out of the beech trunks with high percentage values. In total these groups made more than 74 % of the total collected fauna in each year. During the years the percentage values of *T. bicolor* decreased, *P. ferrugineus* had high percentage values 1994, and *L. navale* reaches >5 % in 1995 for the first time. The calculated emerge rate per m^2 of beech trunks were 690.0 up to 2372.4 animals per m^2 and year (Tab. 2), which is significant lower than that found on spruce trunks (Tab. 1) (Mann-Whitney U-test, $p<0.001$).

The mean values of bark beetles emerged per m^2 and per year out of spruce trunks, and of *Medetera dendrobaena* show Fig. 1. High numbers of *Pityogenes chalcographus* emerged during the first two years after the trunks were blown down and their numbers decreased during the following years (Fig. 1a). With the exception of 1994 the numbers for *Ips typographus* emerged out of spruce trunks show a similar trend. 1993 further trunks were fallen which were intensively used by this species in 1994 and very high numbers of offsprings were produced (Fig. 1b).

With a delay of one year the third bark beetle species *Crypturgus hispidulus* settled the spruce trunks and produced high numbers of offsprings during the following years (Fig. 1c).

On spruce *Medetera dendrobaena* (Dipt., Dolichopodidae) was the only natural enemy which could be found in high numbers. During the first three years 80-90 individuals emerged in mean per m^2 of spruce and per year. The numbers decreased in the following years (Fig. 1d).

The mean values of bark beetles and their natural enemies emerged out of beech trunks show Fig. 2. Two years after the beech trunks were fallen *Taphrorychus bicolor* produced the highest emerging rates per m^2 of beech trunks. They again decreased during the following years (Fig. 2a).

As on spruce trunks *Medetera dendrobaena* was found on beech trunks as well, but in much lower densities. The population increased up to 1993 (one year later as the peak values of *Taphrorychus bicolor*) and decreased again during the following years (Fig. 2b)

On beech trunks two more natural enemies of bark beetles were found since 1992. They did not occur in the first year after the trunks were fallen. With a delay of one year and similar to *Medetera dendrobaena Pityophagus feurugineus* (Col, Nitidulidae) built up his population until it reached 1994 a peak density and decreased again 1995 (Fig. 2c). *Lonchaea seitneri* (Dipt., Lonchaeidae) firstly emerged 1992 out of beech trunks and showed 1994 peak densities which decreased again 1995 (Fig. 2d). These three natural enemies all prey on *T. bicolor* but not on *Xyloterus domesticus*.

The relation prey (bark beetles emerged per m^2 and per year) to predators (natural enemies

Tab. 2. The dominant fauna (%, >5 % of all collected) emerged out of dead beech trunks 1991-1995 (n =11784).

	1991	1992	1993	1994	1995
Acari (excl. Oribatei)	5.1	1.9	0.8	11.9	10.0
Oribatei	15.7	6.8	30.9	15.4	5.4
Collembola	22.5	37.6	33.1	23.5	38.4
Taphrorychus bicolor	36.5	24.1	6.9	1.1	0
Xyloterus domesticus	3.1	18.5	8.6	4.2	8.9
Pityophagus ferrugineus	0	2.5	3.4	12.7	3.6
Lymexylon navale	0	0.1	0.2	0.2	6.1
Sciaridae	0	0.5	4.4	10.6	1.6
Formicidae	0	0	0.05	8.9	0.5
Sum (%)	82.9	92.0	88.35	88.5	74.5
area (m^2)	9000	10800	13800	13800	11000
n (of all)	621	2902	3274	2811	2176
n/m^2	690.0	2687.0	2372.4	2036.9	1978.1

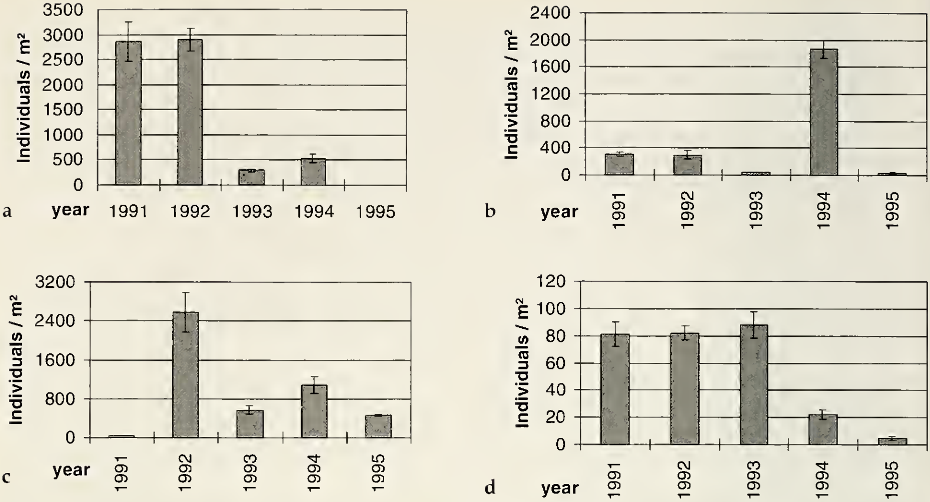

Fig. 1. Numbers of individuals (n/m^2 and s.d.) emerged out of spruce trunks during the years 1991-1995. **a.** *Pityogenes chalcographus* (Col., Scolytidae). **b.** *Ips typographus* (Col., Scolytidae). **c.** *Crypturgus hispidulus* (Col., Scolytidae). **d.** *Medetera dendrobaena* (Dipt., Dolichopodidae).

emerged per m^2 and per year) may be calculated. This relation decreased on beech trunks during the period of investigation (Fig. 3b). On spruce much more bark beetles were present per m^2 and the relation had significantly higher values (Mann-Whitney U-test, $p < 0.001$) and reaches highest values 1994 when there was the high emerging rate of *Ips typographus* (Fig. 3a). Vice versa that means per bark beetle there are many more predators present on beech trunks than on planted spruce trunks. After 3-4 years of degradation of trunks in forests typically the bark fells of the trunks.

Tab. 3 presents the dominant fauna which emerged out of spruce trunks with and without bark on the trunks in 1995. A similar fauna was found and on debarked trunks Empididae (Dipt.) were common. In total on debarked spruce trunks fewer arthropods were found than on trunks with bark (Mann-Whitney U- test, $p < 0.001$).

Tab. 4 presents the dominant fauna which emerged out of beech trunks with and without bark on the trunks in 1995. A deep change in the dominant faunal composition can bee seen and the occurence of species on debarked trunks, which did not settle trunks with attatched bark, e.g. Isopoda, Chironomidae (Dipt.), Sciaridae (Dipt.). As on spruce trunks fewer arthropods were found on debarked beech trunks than on beech trunks with intact bark (Mann-Whitney U-test, $p < 0.001$).

The dipteran fauna composition of dead trunks of spruce and beech may be compared as an example for the diversity found on the trunks. All Diptera were determined on the level of families and

Tab. 3. The dominant fauna (%, >5 % of all) emerged out of dead spruce trunks with and without bark on the trunks 1995.

	without bark	with bark
Oribatei	12.7	10.3
Collembola	68.7	67.8
Crypturgus hispidulus	0	13.8
Empididae	8.0	0
Sum (%)	89.4	91.9
area (m^2)	2600	8200
n (of all)	173	2754
n/m^2	665.3	3358.5

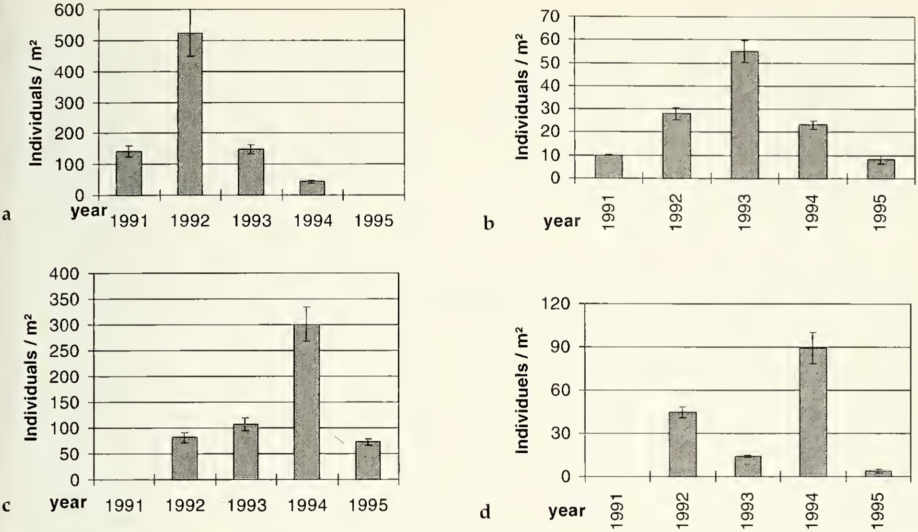

Fig. 2. Numbers of individuals (n/m² and s.d.) emerged out of beech trunks during the years 1991-1995. **a.** *Taphrorychus bicolor* (Col., Scolytidae). **b.** *Medetera dendrobaena* (Dipt., Dolichopodidae). **c.** *Pityophagus ferrugineus* (Col., Nitidulidae). **d.** *Lonchaea seitneri* (Dipt., Lonchaiedae).

on beech 24 different families were found (Tab. 5). With one exeption (Bibionidae) some of them settle spruce trunks as well, but only 13 different families of Diptera were found there. That means a poverished fauna lives on trunks of spruce compared to the fauna on trunks of beech.

Discussion

The study sites consist of a beech forest and of a spruce forest at similar elevations. Those stands are typical for the forests in Germany and in central Europe (Bick 1993). Therefore the fauna of decaying wood is comparable, and represents the present situation in German forests. The method used in this study has several advantages: the wood remains in the forests and is not destroyed; the animals captured alive can be released, if identified and counted in the field; quantitative data of emerged

Tab. 4. The dominant fauna (%) emerged out of dead beech trunks with and without bark on the trunks 1995.

	without bark	with bark
Isopoda	4.6	0
Acari (excl. Oribatei)	0	10.0
Oribatei	0	5.4
Collembola	6.0	38.4
Xyloterus domesticus	0	8.9
Pityophagus ferrugineus	5.3	0
Lymexylon navale	14.6	6.1
Chironomidae	10.0	0
Sciaridae	16.6	0
Sum (%)	57.1	68.8
area (m^2)	2800	11000
n (of all)	150	2176
n/m^2	535.7	1978.1

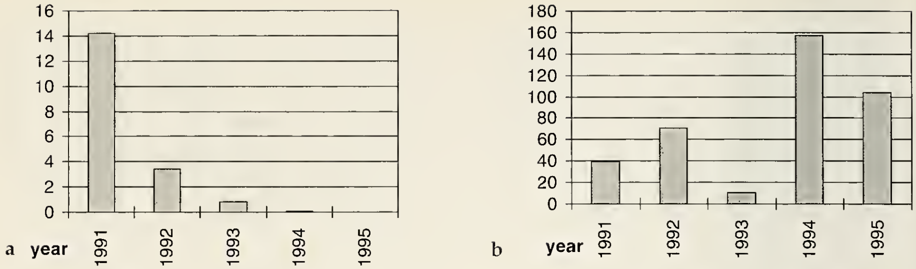

Fig. 3. The relation prey (bark beetles emerged per m² and per year) per predator (species which feed on bark beetles emerged per m² year) on dead trunks of beech (**a**) and of spruce (**b**) during the years 1991-1995.

arthropods per m² of wood are achieved. Bark beetles living on spruce at low elevations have two generations per year (Nicolai 1996) and their ability to produce a high number of offsprings is well known (Postner 1974). If there is produced a high amount of dead spruce wood through any event in spruce plantations mass outbreaks of them can result and this happened several times in German forests during the last decades (Wellenstein 1954). Several methods have been tried to prevent such outbreaks, but no method is presently successful (Zierl 1996), and Vite (1989) described the European struggle to control e.g. *Ips typographus*. During the last years there have been several studies about the influence of bark bettle predators (Dippel 1994, Dippel et al. 1997, Heidger 1994, Nicolai 1995c). During outbreaks of bark beetles these predators are not able to control them mainly because of their feeding capacity and reduced ability to produce two generations per year (Nicolai 1996).

Tab. 5. The families of Diptera found on dead trunks of beech and spruce (1991-1995).

	beech	spruce
Ceratopogonidae	+	
Anisopodidae	+	
Chaoboridae	+	
Chironomidae	+	+
Cecidomyiidae	+	+
Sciaridae	+	+
Mycetophilidae	+	
Culicidae	+	
Psychodidae	+	+
Bibionidae		+
Dolichopodidae	+	+
Empididae	+	+
Phoridae	+	+
Milichiidae	+	+
Lonchaeidae	+	+
Chloropidae	+	
Heleomyzidae	+	+
Aulacigastridae	+	
Chamaemyidae	+	
Pallopteridae	+	
Sphaeroceridae	+	
Periscelidae	+	+
Odiniidae	+	
Platypezidae	+	
Muscidae	+	+
Sum: 25	24	13

Due to the potential of bark beetles living on spruce at low elevation to produce high numbers of offsprings, even in this study high numbers per m^2 of spruce emerged during the first years. After the spruce trunks are settled by bark beetles other organisms are able to settle them as well. Therefore they may be seen as pioneer species and as key species for the breakdown of coarse wood in forest ecosystems. In Norwegian spruce forests Bakke and Kvamme (1993) found 92 species of beetles, which were directly associated with the occurrence of *I. typographus* on spruce trunks. On the other hand this study showed, that only a small fraction of the dipteran fauna was found compared with that found on beech wood at similar elevations.

At my study sites spruce was introduced by man about 100 years ago and comparably few species settled spruce trunks but in high numbers. This corresponds well with the results of Southwood et al. (1982) about insects living on introduced trees.

In main parts of Germany beech forests are the typical natural occurring forest types (Ellenberg 1986). Decaying trunks of beech are settled by different bark beetles and *Taphrorychus bicolor* was found to play an important role. However, this species was never found in such high numbers per m^2 of wood than any bark beetle living on spruce. On the other hand much more different families of flies inhabited decaying wood of beech giving an impression of loss of species diversity through planting of spruce on large areas.

In virgin forests bark beetles are the first colonizers of dead wood and are responsible for the initiation of the decomposition of the trunks. They use their habitat of freshly fallen trunks for one up to three years to produce off springs. The wood is settled by other organisms later. On the other hand that means suitable habitats for the first colonizers of dead trunks must be produced in the forest ecosystem within a time of three years and within a space smaller than the maximum distance the bark beetles are able to fly.

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